Chapter 2

Intraspecific competition

2.1 The nature of intraspecific competition

In order to examine further the way in which the properties of individuals determine population dynamics, we will have to consider a proposition which we have not mentioned explicitly so far, but which is generally taken for granted: that each individual within a population affects, and is affected by, other individuals within the population. Consider, for instance, a thriving population of grasshoppers (all of the same species) in a field of grass. Adult males attract and court adult females by 'stridulating': they rub the insides of their hind legs against the outsides of their hardened forewings to produce a species-specific 'song'. If a male manages to attract, court and inseminate a female, he will have made some contribution to the next generation; and the more females he manages to inseminate, the greater this contribution will be. The most successful or fittest males within a population are those which make the greatest contribution. A solitary male amongst many females in the population might eventually inseminate every one of them. But if there are several males in the population, then they will be *competing* with one another for the females' attentions, and each will inseminate fewer females than he would have done had he been alone. The more males there are, the more intense this intraspecific competition will be; and the general effect will be to reduce the males' contributions to the next generation.

Subsequently, the inseminated grasshoppers will have eggs to lay. For this they require bare soil, which may, in a grassy field, be quite rare. More to the point, they require bare soil not already occupied by another female. They can increase their contribution to the next generation by increasing the number of eggs they lay. But the more *competing* females there are, the longer it will take each one to find an appropriate site,

and the fewer eggs she will lay per unit of time. Moreover, along with this increased expenditure of time will go an increased expenditure of energy. This will lead to a decrease in the energy available for egg development, and also a decrease in general viability, leading to a possible shortening of total life span. These, in their turn, will lead to a decrease in the number of eggs laid; and the more competing females there are, the greater this decrease will be.

Of course, in order to live, grasshoppers (male and female) must consume food (grass) to provide themselves with energy, but they must also expend energy in the process of finding and consuming the food. Each grasshopper will frequently find itself at some spot where there had previously been a palatable blade of grass—before that is, some other grasshopper ate it. Whenever this happens the first grasshopper must move on; it must expend more energy than it would otherwise have done before it takes in food. Once again, this increased energy expenditure will lead on the one hand through increased mortality and on the other hand through decreased rates of development, to a decreased contribution to the next generation. So the more competitors there are, the more 'moving on' each grasshopper will have to do, and the greater the decrease in contribution will be.

Considering the same hypothetical ecosystem, we can turn now to the grass itself. (We will assume, for simplicity, that it is all of one species, although in practice this is very unlikely to be so.) The contribution of an individual grass plant to the next generation will be dependent on the number of its progeny which eventually develop into reproductive adults themselves. An isolated seedling in fertile soil will have a very good chance of developing to reproductive maturity, and will also be likely to reproduce vegetatively, consisting (as a result) of multiple copies of the simplest plant form. However, a seedling which is closely surrounded by neighbours (shading it with

their leaves and depleting its soil with their roots) will be very unlikely to survive at all, and will almost certainly be small and simple. The more competing individuals there are, the more likely it is that seedlings will find themselves in the latter, rather than the former, situation. Increases in density will, therefore, lead to decreases in the contributions of individuals to the next generation.

2.2 Three characteristics of intraspecific competition

Certain common features of intraspecific competition have obviously emerged. The first of these is that the *ultimate effect* of competition is a decreased contribution of individuals to the next (or, in fact, to all future) generations: a decrease, that is, from the potential contribution that the individual would have made had there been no competitors.

In some cases—stridulating males competing for females, for instance—the connection between competition and contributions to future generations is obvious and direct. With grass seedlings competing for growth resources, however, or with grasshoppers competing for food, the connection is slightly less direct, since competition leads to a decrease in survivorship and/or fecundity. Nevertheless, in terms of ultimate effects, male grasshoppers competing for females, seedlings competing for light and grasshoppers competing for food are all essentially equivalent. Intraspecific competition acts more or less directly on either survivorship or fecundity, or on both, but in all cases it decreases contributions to future generations.

From a practical point of view, however, this is not quite enough. Competition must not only be likely; it must also manifest itself in measurable decreases in survivorship, fecundity or some other, less direct characteristic. Only then have we the right to conclude that it is occurring.

The second common feature of intraspecific competition is that the resource for which the individuals are competing must be in limited supply. Oxygen, for instance, although absolutely essential, is not something for which grasshoppers or grass plants need compete. Nor *necessarily* is space, food or any of the other resources we have discussed so far. They are only competed for if they *are* in limited supply.

The third feature of intraspecific competition is *reciprocity*. In other words the competing individuals within a population are all essentially equivalent (in contrast to the situation of a predator eating its prey, in which the predator is inherently the inflictor of the adverse effect and the prey inherently the receiver). Of course, in any particular case intraspecific competition may be relatively one-sided: the strong early seedling shading the stunted late one; the 'resident' egg-laying grasshopper causing the later arrival to move on. However, despite this, because the early/late or resident/non-resident roles might easily be reversed, the competing individuals are *inherently* equivalent.

2.3 Density-dependence: a fourth characteristic

The fourth and final feature of intraspecific competition is that the effect of competition on any individual (i.e. the *probability* of an individual being adversely affected) is greater, the greater the number of competitors there are. The effects of intraspecific competition are, therefore, said to be *density-dependent*. Not surprisingly, they can be contrasted with density-independent effects, yet the point of contrast is very often confused. This can be avoided by reference to Fig. 2.1 (after Solomon, 1969). In Fig. 2.1a the *number* of deaths is dependent on density (and, indeed, increases with density) in each of the four lines, but of these four, only three show density-dependent effects. In the fourth, the *proportion* of the population dying (or the *probability* of an individual dying) remains constant, even though the number dying increases with density: the *rate* of mortality is density-independent. Figure 2.1b, which portrays precisely the same situation as Fig. 2.1a, makes this abundantly clear. Of course, in reality, the points leading to the density-independent plots will not all lie exactly on the straight lines. They may, in fact, be very widely spread on either side of them. However, this would not alter their essential feature: with density-independent mortality, there is *no tendency* for the mortality-*rate* to increase with increasing density. The analogous situation for
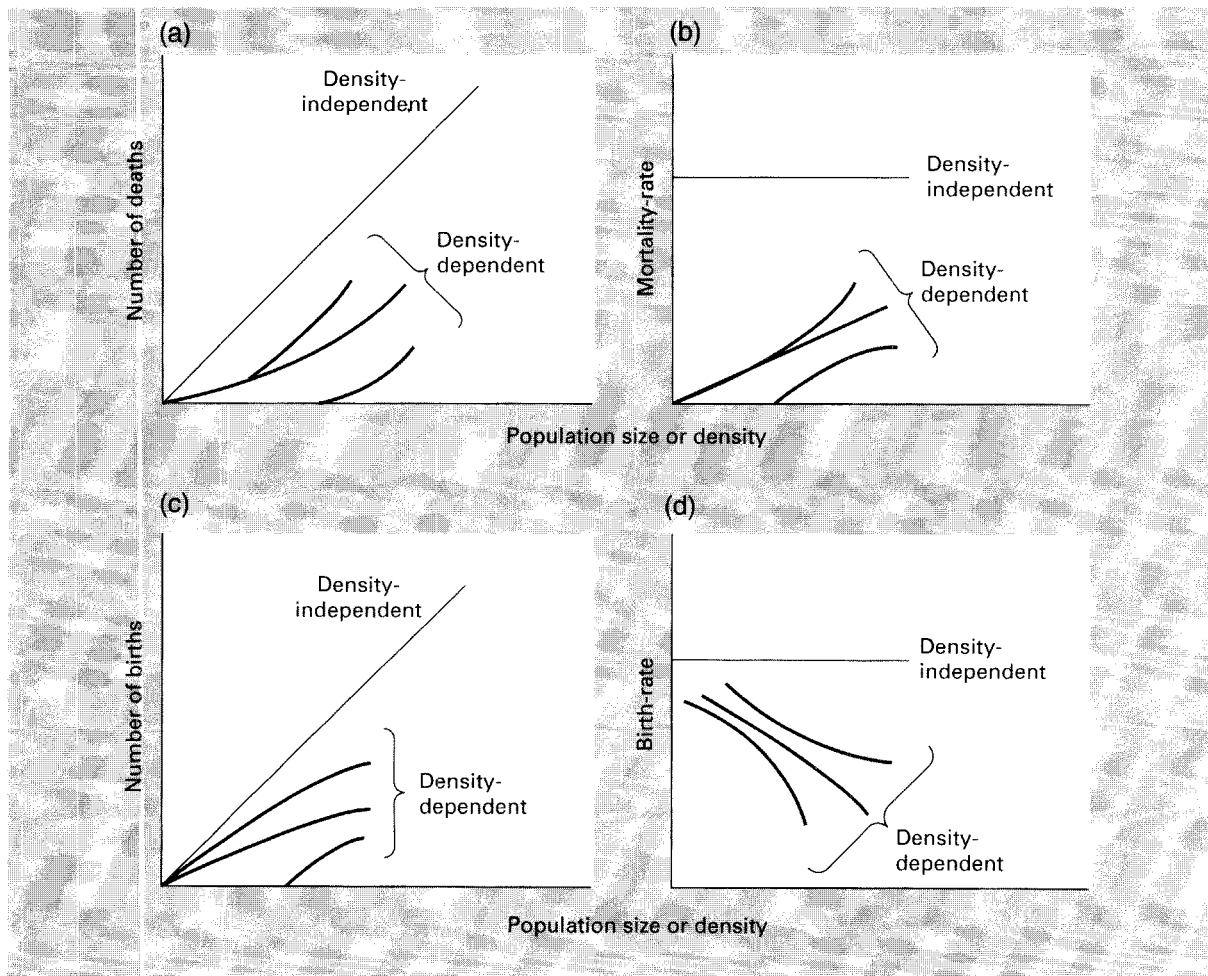
Fig. 2.1 Density-dependent and density-independent death (a) and (b), and birth (c) and (d). The vertical axes in (a) and (c) are numbers; those in (b) and (d) are rates. (After Solomon, 1969.)

fecundity is illustrated in Figs 2.1c and 2.1d.

Intraspecific competition and density-dependence are obviously bound closely together; whenever there is intraspecific competition, its effects—whether on survival, fecundity or a combination of the two—is density-dependent. However, not all density-dependent effects are the result of intraspecific competition. Chapter 4 on interspecific competition, and Chapter 5 on predation, parasitism and herbivory will

make this quite clear. Nevertheless, all density-dependent effects do share a *tendency to regulate population size.*

We have already suggested (in Chapter 1) that such regulation is extremely widespread, and the subject will be examined in greater depth in Chapter 6; but three pertinent comments can be made now. First, 'regulation' refers to the ability to decrease the size of populations which are above a particular level, but to allow an increase in the size of populations below that level. This particular population level will, therefore, be a point of equilibrium. Populations below it increase, populations above it decrease, and populations actually on it neither increase nor decrease: popula-
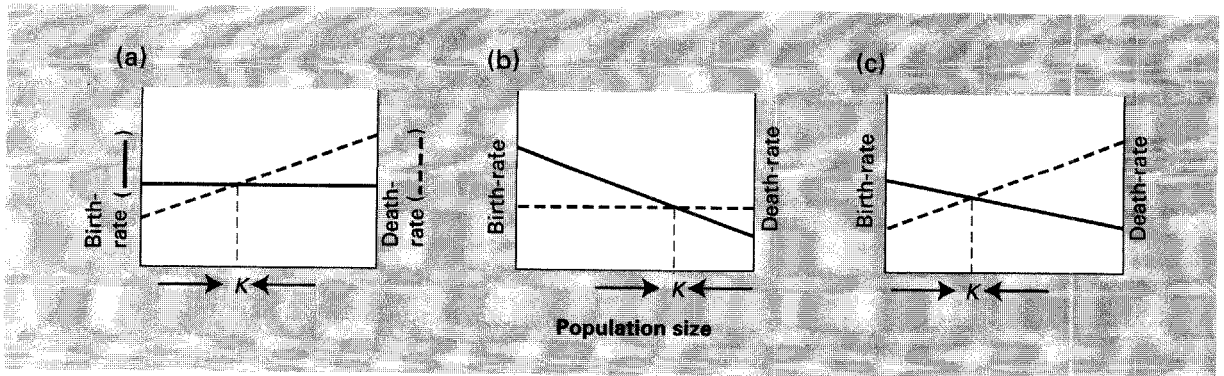
Fig. 2.2 Population regulation with (a) density-independent birth and density-dependent death, (b) density-dependent birth and density-independent death, and (c) density-dependent birth and density-dependent death. Population size increases when birth-rate exceeds death-rate below the carrying capacity, K; and decreases when death-rate exceeds birth-rate above K. K is, therefore, a stable equilibrium.

tion size is subject to negative feedback (Fig. 2.2). In the case of the effects of intraspecific competition, this equilibrium level is often called the 'carrying-capacity' of the population. In reality, however, no single carrying-capacity can ever characterize a natural population: most aspects of its environment are far too variable, and its own behaviour is never wholly predictable. For this reason 'regulation' may, more reasonably, be taken as the ability to act on a very wide range of starting densities, and bring them to a much narrower range of final densities.

Second, the word 'tendency' is used advisedly. If a density-dependent effect is not operative at all densities, or is not operative under all environmental conditions, is weak, or happens after a time delay, then the effect—although density-dependent—may not *actually* regulate population size. Similarly, if there are several density-dependent factors acting on a population, then each factor alone may be incapable of regulating the population, even though each *tends* to do so.

Third, all density-dependent *effects* are the result of a density-dependent *factor* acting through a density-dependent *process*. Until now only one density-dependent process has been considered (intraspecific

competition), invoked by various density-dependent factors: food, space and so on. It should be remembered, however, that the effects of intraspecific competition can easily be discussed without specifying the factor involved; and these effects—on either mortality or fecundity—can even be measured. Yet if, ultimately, we are to understand the dynamics of a population, we must identify the density-dependent factor itself.

2.4 Scramble and contest

The density-dependent effects of intraspecific competition are of central importance in the dynamics of natural populations, but so far they have only been outlined. We have still to describe the precise effects that intraspecific competition can have on the quantity *and* quality of individuals within a population. Of course, competitive interactions do not all conform to precisely the same pattern. On the contrary, there is a whole spectrum of interactions, varying in their underlying biological causes, and in their effects on the quantity and quality of individuals; but in order to appreciate this variety, it will be useful to have certain standards against which actual examples can be matched. The most appropriate standards are the extreme forms of competition described by Nicholson (1954b): 'scramble' and 'contest'.

The essential features of scramble and contest are illustrated in Figs 2.3 and 2.4 respectively (adapted from Varley et al., 1975). It is particularly important to note that Figs 2.3b and 2.4b make use of the 'k-values'
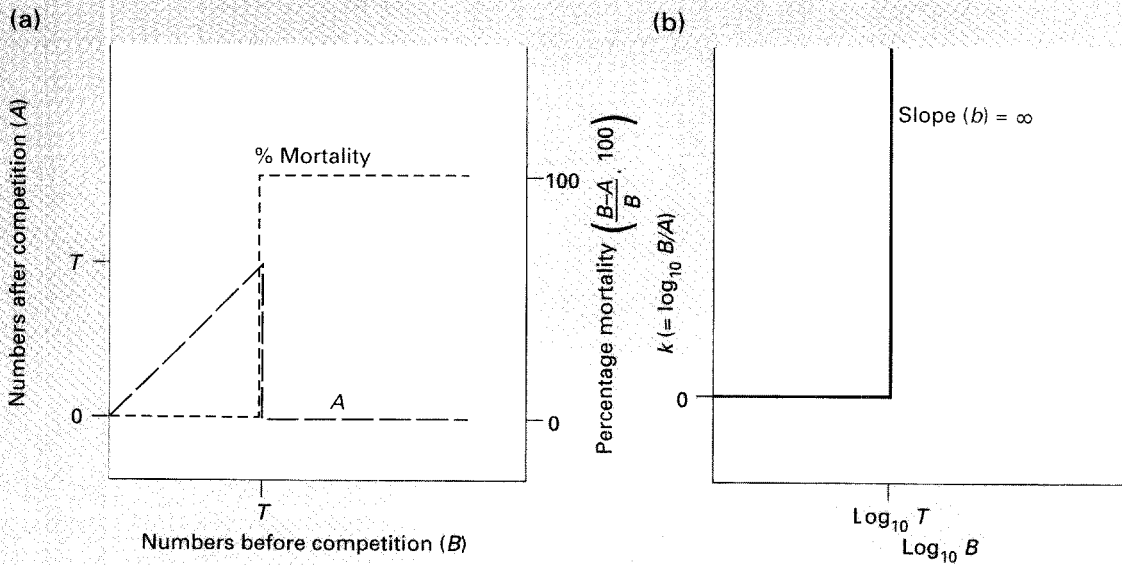
Fig. 2.3 Scramble competition. Mortality relationships (a) in terms of numbers surviving and percentage mortality, and (b) in terms of k plotted against the logarithm of density.

described in Chapter 1. In both cases there is no competition at all at low densities: all individuals have as much resources as they need, and all individuals need and get the same amount (% mortality = 0; $A = B$; $k = \log_{10} B/A = 0$). Above a threshold density of T individuals, however, the situation changes. In scramble competition (Fig. 2.3), all the individuals still get an equal share, but this is now less than they need, and as a consequence they all die. The slope, b, of Fig. 2.3b therefore changes suddenly from zero to infinity as the threshold, T, is passed. Conversely, in contest competition (Fig. 2.4) the individuals fall into two classes when the threshold is exceeded. T individuals still get an equal and adequate share of the resource, and survive; all other individuals get no resource at all, and therefore die. There are always just T survivors in contest, irrespective of the initial density, because mortality compensates exactly for the excess number of individuals. In Fig. 2.4b the slope changes at the threshold from zero to 1; *this b-value of 1 is indicative of*

the exact compensation of contest competition.

Scramble and contest can also be seen in terms of fecundity. Below the threshold there is no competition, and all individuals produce the maximum number of offspring. Above the threshold, scramble leads to the production of no offspring whatsoever; while contest leads to T individuals producing the maximum number of offspring and the rest producing none at all.

Our 'standards' of competition have now been defined. In terms of the quantity of individuals, neither scramble nor contest are effective below some threshold; but above this threshold scramble reduces numbers to zero, while contest maintains a numerical constancy. In terms of quality, both scramble and contest allow only two classes of individual: those getting all they require and therefore surviving (or producing the maximum numbers of offspring), and those getting less than they need and therefore dying (or producing no offspring at all). The difference is that in scramble all individuals move suddenly from the first class to the second at threshold; while in contest there are still T individuals in the first class, even when threshold is exceeded.
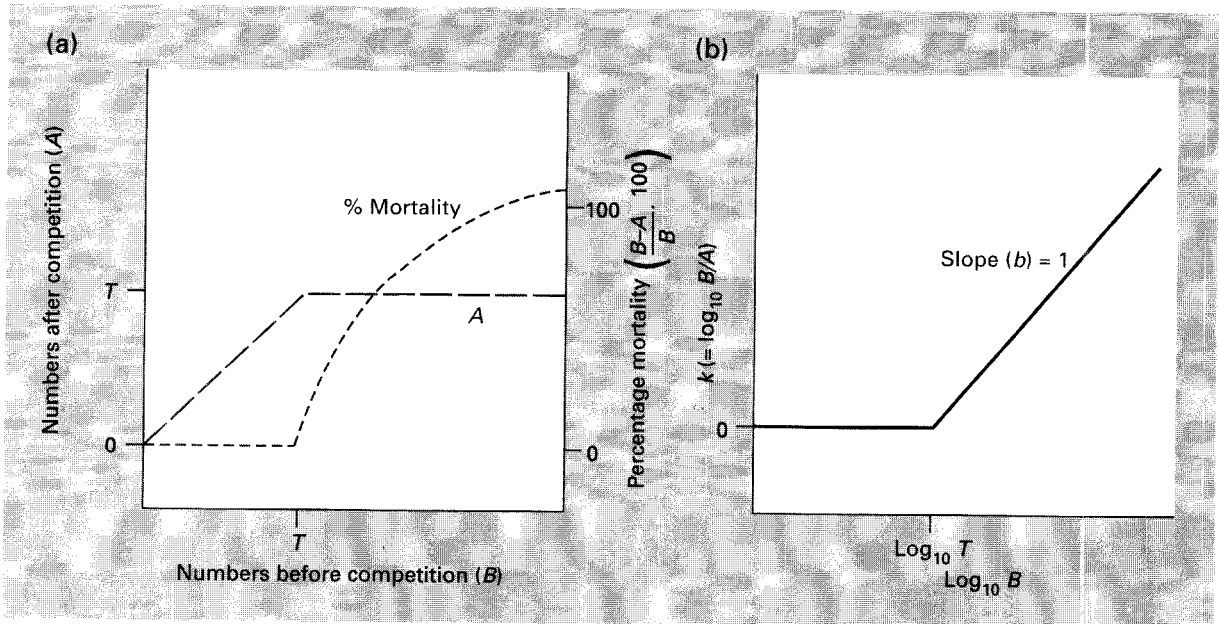
Fig. 2.4 Contest competition. Mortality relationships (a) in terms of numbers surviving and percentage mortality, and (b) in terms of k plotted against the logarithm of density.

2.5 Actual effects of intraspecific competition

2.5.1 Palmblad's data

Having described these hypothetical extremes, it is appropriate to examine some actual examples. Studies of plants indicate the inadequacies of 'scramble' and 'contest' particularly clearly.

Palmblad (1968) undertook an experimental study on the effects of intraspecific competition on several species of weed. Some of his results are summarized in Table 2.1 and Fig. 2.5. They refer to two annual species, *Capsella bursa-pastoris* (Shepherd's purse) and *Conyza canadensis* (Canadian fleabane), and the perennial, *Plantago major* (plantain). Palmblad's procedure was simply to sow seeds of each species under controlled conditions at a range of densities (1, 5, 100 and 200 seeds per pot), and then keep a careful record of their subsequent progress. As Table 2.1 shows, he was able to compute the percentage of seeds that

actually germinated and produced seedlings ('germination' in Table 2.1), the percentage that subsequently died before setting their own seed at the end of the summer, and the percentage that remained alive but failed to reproduce ('vegetative' in Table 2.1). The number of seeds produced by each individual was then counted, and the 'mean number of seeds per reproducing individual' and the 'total number of seeds per pot' computed. Finally, the total dry weight of plants, both reproductive and vegetative, was measured for each pot.

The results are also summarized in Fig. 2.5, where the k-values of the various processes are plotted against the $\log_{10}$ of the sowing density (as they were in Figs 2.3b and 2.4b). $k_{germination}$, $k_{mortality}$ and $k_{vegetative}$ are all self-explanatory; $k_{fecundity}$ refers to the reduction in the number of seeds produced per individual, $\log_{10}$ (maximum seeds/actual seeds); while k_{total} refers to the reduction in the total number of seeds produced, but is also the sum of all the other k-values.

The first point to note is that, almost without exception, the 15 plots in Fig. 2.5 show k increasing with density. The density-dependent nature of the various responses of these plants to intraspecific competition is, therefore, immediately confirmed. It is

Table 2.1 Aspects of Palmblad's (1968) experimental data on intraspecific competition in three species of weed.

	Capsella bursa-pastoris					Plantago major					Conyza canadensis				
Sowing density	1	5	50	100	200	1	5	50	100	200	1	5	50	100	200
% Germination	100	100	83	86	83	100	100	93	91	90	100	87	56	54	52
% Mortality	0	0	1	3	8	0	7	6	10	24	0	0	1	4	8
% Reproducing	100	100	82	83	73	100	93	72	52	34	100	87	51	42	36
% Vegetative	0	0	0	0	2	0	0	15	29	32	0	0	4	8	8
Dry weight (g)*	2.01	3.44	4.83	4.51	4.16	8.05	11.09	13.06	13.74	12.57	12.7	17.24	17.75	16.66	18.32
Mean number of* seeds/reproducing individual	23 741	6102	990	451	210	11 980	2733	228	126	65	55 596	13 710	1602	836	534
Total number of seeds	23 741	30 509	40 311	37 196	30 074	11 980	12 670	8208	6552	4420	55 596	59 625	40 845	35 264	38 376
$k_{germination}$	0	0	0.08	0.07	0.08	0	0	0.03	0.04	0.05	0	0.06	0.25	0.27	0.28
$k_{mortality}$	0	0	0.01	0.02	0.04	0	0.03	0.03	0.05	0.13	0	0	0.01	0.03	0.08
$k_{vegetative}$	0	0	0	0	0.02	0	0	0.08	0.19	0.29	0	0	0.03	0.08	0.08
$k_{fecundity}$	0	0.59	1.38	1.72	2.05	0	0.64	1.72	1.98	2.27	0	0.61	1.54	1.82	2.02
k_{total}	0	0.59	1.47	1.81	2.19	0	0.67	1.86	2.26	2.74	0	0.67	1.83	2.20	2.46

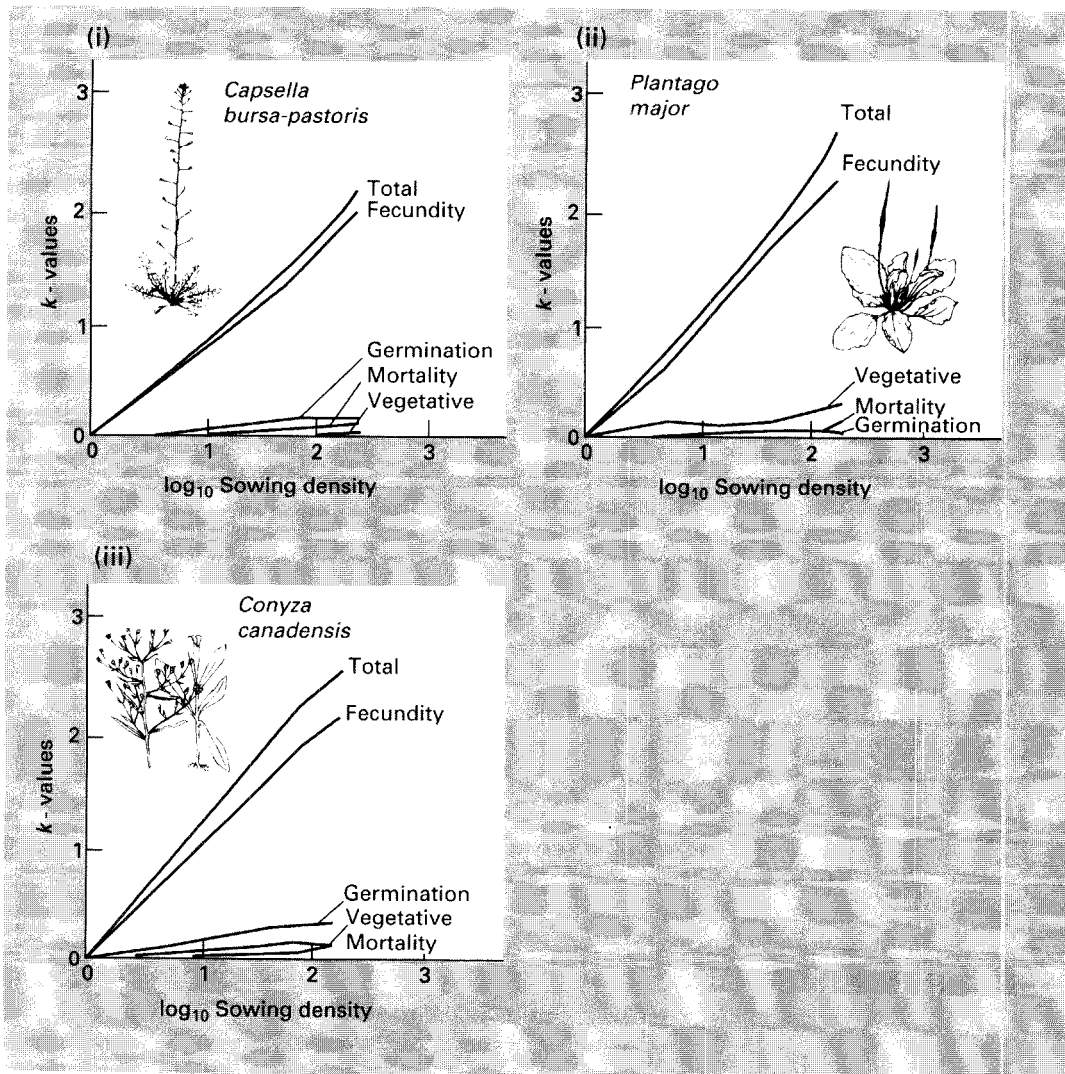*These data are averages of three individual pot values.

Fig. 2.5 The varied effects of intraspecific competition: experiments on populations of three species of weed. (Data from Palmblad, 1968.) For further discussion see text.

also apparent, however, that the sudden threshold, characteristic of scramble and contest, is generally lacking in these real examples. Instead, as density increases, the slopes tend to increase gradually. This, not surprisingly, is characteristic of many real examples: as density increases, so the *intensity* of competition increases. One reason for this is that,

because the plants were not spaced with total regularity, different plants experienced different degrees of crowding. Another is that the plants themselves were inherently (i.e. genetically) different. Other reasons will soon become apparent.

In all three species, intraspecific competition exerted its density-dependent effects on the proportions germinating, surviving and remaining vegetative, and in each case the plants fell, as a result, into one of two categories: those that 'did', and those that 'did not'. With reproduction, however, the situation was far

more complex, the density-dependent effects of intraspecific competition were no less obvious, but the response was very far from being all-or-none. Instead, the mean number of seeds produced per individual varied continuously throughout an almost 200-fold range in *Plantago major*, and an approximately 100-fold range in *Capsella bursa-pastoris* and *Conyza canadensis*. This plasticity of response—admittedly exemplified by seed production in plants—is common throughout both the plant and animal kingdoms. Intraspecific competition leads not only to quantitative changes in the numbers surviving in populations, but also to qualitative changes in those survivors; and these progressive decreases in quality as density increases contribute significantly to the increasing intensity of competition.

In Palmblad's experiments these qualitative changes were not confined to average seed production. Despite the considerable variation in the density of surviving plants, the total dry weight for each species, after an initial rise, remained remarkably constant with increasing density. In other words, at higher densities individual plants were smaller. There was 'compensation' so that the final 'yield' remained largely unchanged.

Of course, the qualitative changes in dry weight and seed production are closely connected: smaller plants produce fewer seed. This, as Table 2.1 shows, leads to a comparative constancy in the total number of seeds produced. Thus, the regulatory tendencies of intraspecific competition are amply illustrated; despite a 200-fold range of sowing densities, the range of seed output is only 1.4 in *Capsella bursa-pastoris*, 2.9 in *Plantago major* and 1.7 in *Conyza canadensis*. That such regulation does indeed occur is illustrated in another way in Fig. 2.5. Remember that in contest competition there was an absolute constancy of output illustrated by a slope (b) of 1. In Fig. 2.5 the slopes of the three graphs for k_{total}, taken over the whole range, are also close to 1, indicating the near-constancy of output already noted. The resemblance to contest, however, is only superficial. In contest, constancy is achieved by a constant number of survivors all producing the same number of offspring. In Palmblad's experiments, as in real examples generally, the near-constancy of output

was achieved by a variable number of survivors producing a variable number of offspring.

Looking at these graphs more closely, we see that at lower sowing densities—below 50 in *Capsella*, and below 5 in *Conyza* and *Plantago*—the slopes of the k_{total} graphs are, in fact, less than 1. This indicates *under*-compensation (i.e. less than the *exact* compensation of $b = 1$); although there is a reduction in individual output, this is not enough to compensate for the increasing density, and the total output increases (Table 2.1). Conversely, at higher densities (with the exception of *Conyza* between 100 and 200), there is *over*compensation; the reduction in individual output more than compensates for the increased density, and total output decreases. This is indicated by a slope greater than 1. In each species, therefore, the yield of seed reaches a peak towards the middle of the density range. Its precise position is indicated by the point on the graph where the slope equals 1 exactly. Thus, not only do the graphs in Fig. 2.5 show the degree of compensation resulting from competition, they also indicate the sowing density that would maximize the final yield of seed. For commercially valuable crops, such graphs may be of considerable importance.

Finally, it is apparent from Fig. 2.5 that the relative importance of germination, mortality and so on in regulating output is different in the three species. This is made particularly clear by the fact that k_{total} (the total effect) is the sum of all the other k-values. In *Capsella bursa-pastoris* the effects of competition are almost entirely on the growth, and therefore the seed production, of surviving individuals. In *Conyza canadensis* seed production is also of primary importance, but a substantial proportion of the total effect is the result of reduced rates of germination. Conversely, in *Plantago major* the tendency to remain vegetative and (to a lesser extent) mortality play an important role; this is no doubt associated with the perennial habit. Thus, although the end-results are similar in the three species, the ways in which they are achieved are rather different.

In summary, then, we have learnt a great deal that is of general relevance from this limited example. Typically, intraspecific competition affects not only the quantity of survivors, but their quality as well, which

becomes more and more affected as density increases. This, combined with the variability of both environment and individuals, means that there is usually no sudden threshold for competition in nature. Rather, it increases gradually over an extended range. Palmblad's experiment also reiterates that the ultimate effect of intraspecific competition, acting through survival and fecundity, is on the contributions to future generations; that individuals are affected reciprocally; that intraspecific competition tends to regulate populations; and that the effects can be measured without the unequivocal identification of the resource in limited supply.

2.5.2 Competition in plants: a deeper look

Palmblad's experiments also illustrate two important interlinked events that can occur when plant populations are grown in resource-limited environments. The first is that the size of individuals (as measured for instance by individual biomass or seed production) is reduced; the other is that ultimately mortality may ensue. These events occur along a spectrum of competitive effects on the growth of individual plants. The extremities are the death of the individual (growth and maintenance ceased) and unconstrained growth (growth rate = maximum for that environment). The 'in between' is a reduced growth rate (less than maximum) which is reflected at some point in time (harvest of the plant) in a reduced plant size.

Evidence for the density-dependent effects of competition can be examined at various levels: at the level of the population itself, amongst individuals within the population and within individual plants. We will follow this progression, which is, perhaps not surprisingly, the way our scientific understanding has historically developed. Finally, we attempt to integrate our understanding of the whole process.

Figure 2.6 shows the two general forms of 'yield-density' relationship that have emerged from the wealth of studies conducted by agronomists and ecologists. The figures relate population density *before* the action of competition—often the number of plants sown as seed or planted—to population density (yield)

after the action of competition, always on a constant area basis. This yield may be measured in a variety of ways either as a direct fitness component (e.g. seed produced) or less directly as biomass, either of the total plant or some of its constituent parts. The form of response is either : (i) *asymptotic* (Fig. 2.6a) where yield per unit area levels off with increasing density (i.e. perfect compensation; constant final yield); or (ii) *parabolic* (Fig. 2.6b), where a maximum yield is reached at an intermediate density before falling at high densities (i.e. overcompensation). From these examples, we can see (as we might expect) that the influence of adding more resources for growth (by fertilizer) increases the size of the population, measured as the height of the asymptote or peak of the parabola.

The asymptotic constant yield response, which develops progressively, can best be explained by looking at the changes in the population with time and the performance of individuals. Soybeans grown over a 1000-fold density range show particularly well (Fig. 2.7a). At sowing (day 0), yield per unit area and density are directly proportional to one another: the yield is the weight of the seed sown! With time this linear proportionality disappears, as plants grow to sizes at which they interfere with one another, the interference occurring first at the highest density. The yield curves therefore display a successively pronounced shoulder as the linear proportionality disappears, but this in its turn is replaced (after 119 days) by a horizontal yield curve when final yield is independent of original population size. Compensation by individuals on this sort of scale (here 10 and 1000 plants m^{-2} yielding the same biomass after 119 days) is a direct reflection of the enormous *plasticity* that species with modular growth possess. Such plasticity has been shown to occur in a wide range of species including pine trees, grasses and herbs. Re-examining the same data, but from the viewpoint of an average individual soybean plant, shows us that compensation through adjustment of the performance of individuals is indeed occurring. From being initially independent of density (at day 0), the average weight of a plant becomes increasingly related to it (Fig. 2.7b). Plants at low density (10 m^{-2}) achieved a final mean weight of
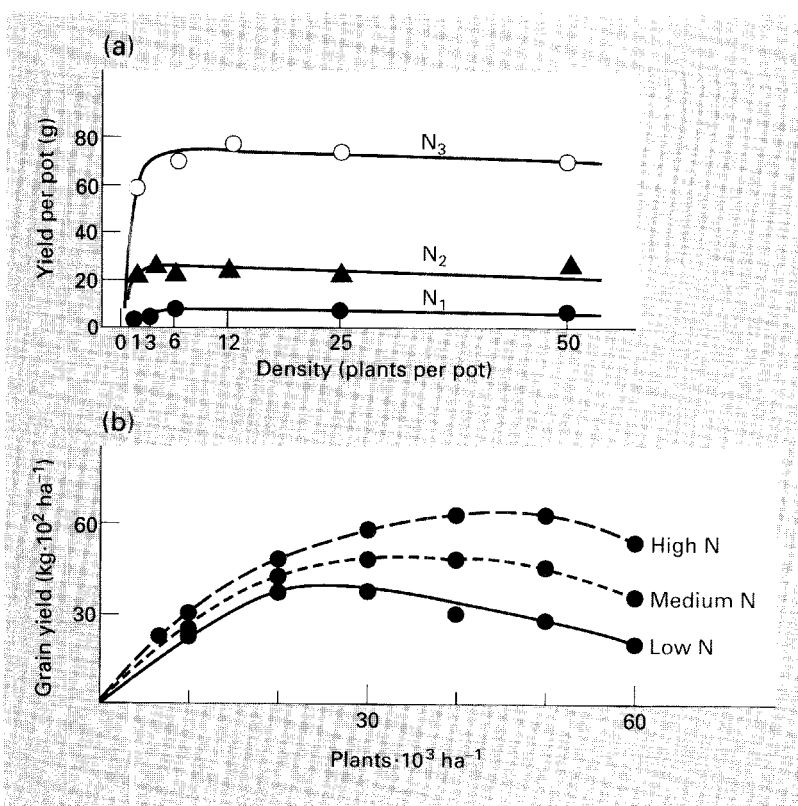
Fig. 2.6 Illustrative yield-density relationships in plants. (a) *Bromus uniloides* at three nitrogen fertilizer levels. (From Donald, 1951.) (b) *Zea mays* at three fertilizer levels. (Data of Langer *et al.*, 1956; from Willey & Heath, 1969.) See text for explanation.

nearly 70 g whereas those in populations of 50 m^{2} were only 14 g. Moreover, it is important to realize that these adjustments occurred in the absence of mortality. Yield density experiments in both agriculture and forestry have frequently reaffirmed that in many situations (species and environments) mean yield per plant is inversely proportional to density or that total yield per unit area is independent of density. This observation has been described as the 'law of constant final yield' (Kira *et al.*, 1953).

How then can we explain situations in which the law of constant final yield is not obeyed (e.g. Fig. 2.6b), and yield at high densities declines from an intermediate optimum? This question cannot be fully answered for all cases, but two cogent possible explanations are: (i) plant mortality does occur during the course of competition, but the surviving plants are unable to exploit fully resources freed by the death of

other members of the population; and (ii) species respond *differentially* according to their developmental stage. To appreciate these explanations we must first give further consideration to two features of plant growth.

The first is that the production of flowers and hence seeds requires the differentiation of floral meristems. These may arise from the permanent conversion of vegetative meristems, or they may be borne laterally on an axis that retains a vegetative meristem at its tip. This difference leads to a dichotomy in growth form. Species may show *indeterminate* growth, bearing flowers at nodes laterally to growing axes and thus retaining the potential for indefinite vegetative extension. In contrast, species may show *determinate* growth, where the conversion of vegetative meristems into floral structures prohibits further vegetative development. Conversion may be triggered by changes
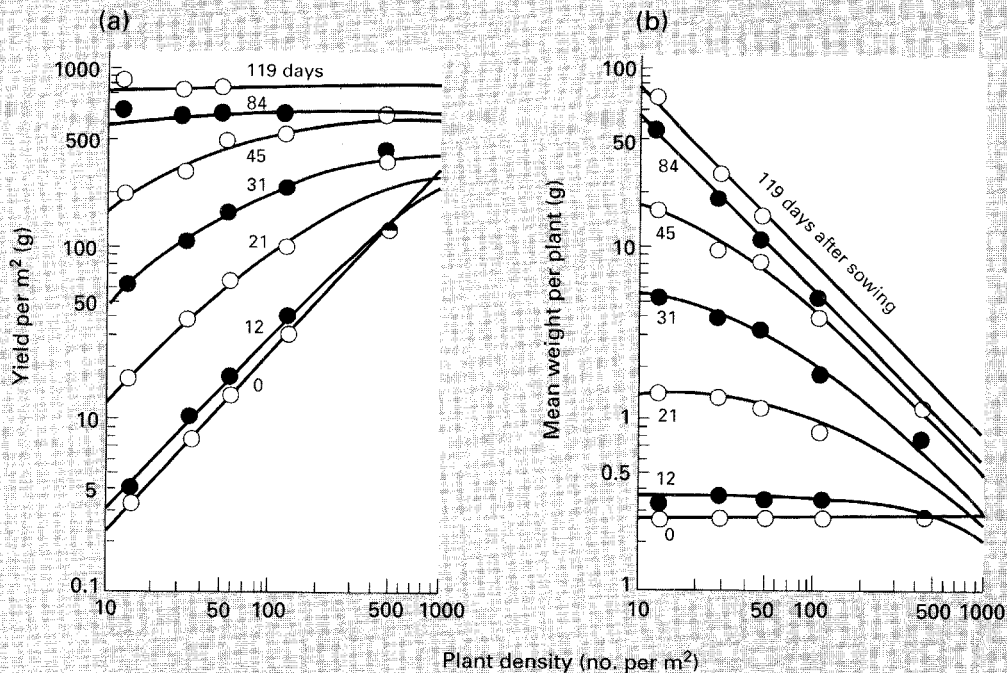
Fig. 2.7 Yield-density relationships in soybean *Glycine max*: the progressive changes with time (a) on a unit area basis, and (b) per plant. (From Shinozaki & Kira, 1956; after Harper, 1977.)

in day length and/or temperature (vernalization), or may be genetically fixed.

The second feature that we must consider is how yield is formed. In the case of seed, it requires the production of a range of plant parts, i.e. *the components of yield* (e.g. stems, flower-bearing branches, flowers, pods and seeds). All components may respond to density but as successive components are produced we might expect the type of density response to change.

Populations of cultivated sunflowers (*Helianthus annus*) provide us with an illustration of one type of yield-density response (Fig. 2.8a) in which there is overcompensation. In this sunflower, plants usually bear a single large capitulum (flower head). This develops from the terminal meristem when the plant

is young, before the influence of competition has become marked. Thus, the response to density-induced resource limitation cannot be a reduction in capitulum number. Instead it is etiolation of the plant, and reduction both in the proportion of flowers within the capitulum that set mature achenes (seeds) and the size of those achenes. In the field bean (*Vicia faba*) on the other hand (Fig. 2.8b) responses to density are seen at all developmental stages in the production of seeds. Part of the response is a reduction in the number of stems per plant and flowers per stem, and part is the abscission of flowers and pods. The overall outcome of this plasticity is near constancy in seed population size per unit area. One further contrast may be drawn from this example. In *Helianthus*, individual seed weight declined markedly with plant density, whereas in *Vicia* it remained constant. The former response, however, is the exception to the generally observed phenomenon of homeostasis in seed size in response to density. (Wild progenitors of *Helianthus* absorb density stress by reducing the
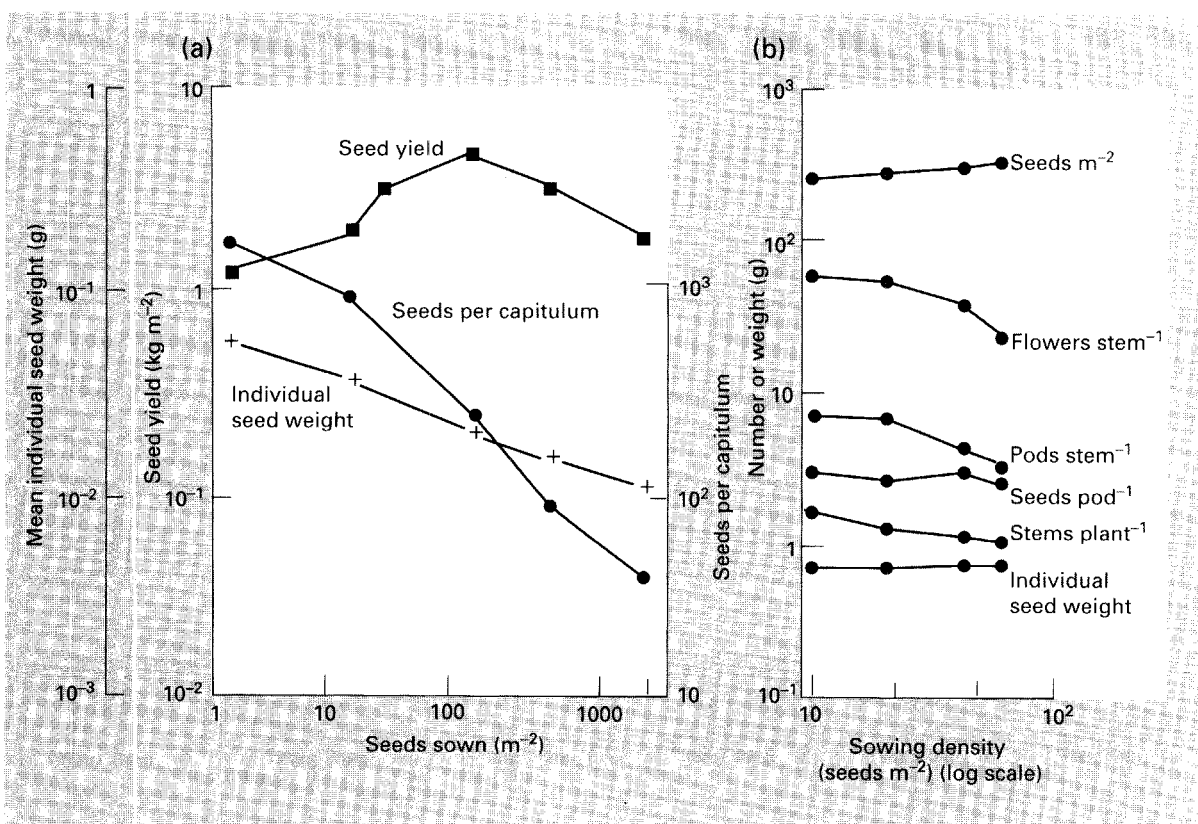
Fig. 2.8 Yield-density responses in (a) cultivated sunflowers (data replotted from Clements *et al.*, 1929), and (b) field bean (data from Hodgson & Blackman, 1956).

numbers of branches and capitula, preserving constancy of seed weight; Bradshaw, 1965.)

Sunflowers and field beans provide us with clear illustrations of some of the responses of determinate and indeterminate growth forms to intraspecific competition but we should not assume that yield responses can be inferred from knowledge of the growth form of the plant. Final seed yield is the product of a number of yield components each of which may respond to density in a specific way. Figure 2.9 illustrates these yields within a species (field bean) in which determinate and indeterminate growth forms have been selected (Pilbeam *et al.*, 1991). In the determinate form all yield components (stems/plant, nodes/stem, pods/node, seeds/pod) tended to decline systematically with

increasing density, whereas in the indeterminate form yield component responses were noticeably more varied.

Many annual grasses, as exemplified by wheat (*Triticum aestivum*), exhibit a density response that is of a combined form. Seed production in wheat is the product of the number of fertile tillers per plant and the number of grains (seeds) per ear: a fertile tiller bears only one ear which may vary in size and thus in floret and seed number. Prior to flowering and ear formation, density stress is reflected in reduced vegetative biomass and plant parts, but afterwards it is reflected in the size of the ears. This is shown (Fig. 2.10) by a field experiment of Puckridge and Donald (1967) who grew wheat over a 1000-fold density range and followed the course of grain yield development. After 14 weeks growth, plants had received stimuli for flowering. At this time the number of tillers per plant was strongly density-dependent
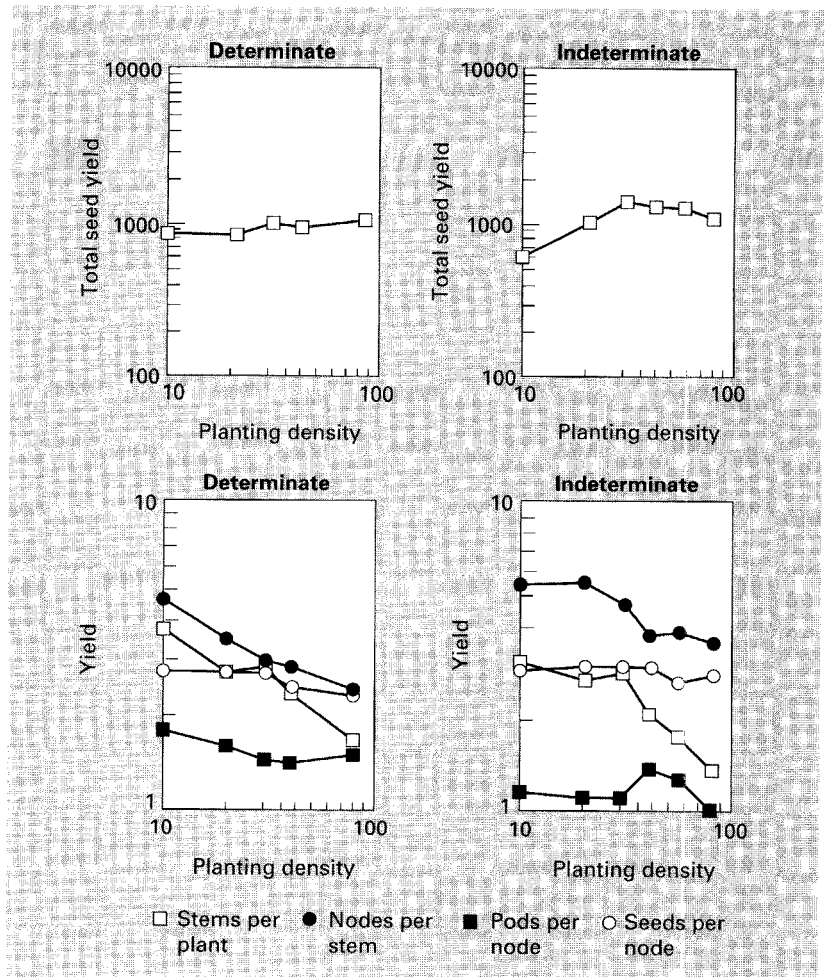
Fig. 2.9 Seed yield and yield component responses to density in determinate and indeterminate growth forms of *Vicia faba*. (Data from Pilbeam *et al.*, 1991.)

(line A in Fig. 2.10). During ear formation (17 weeks) and subsequently through to maturity (26 weeks) the number of tillers changed little and the number of fertile tillers was a constant fraction of the total. However, the effects of density were reflected in changes in ear weight (Fig. 2.10, lines D and E). These two phases in density adjustment, therefore, resulted in a constant individual seed weight at harvest and in an asymptotic yield response per unit area up to 100 plants m^{-2}. Conversely, the depression of yield at the highest sowing density in this experiment was a consequence of density-induced mortality (note the end-points of lines C, E and G are displaced to the left).

This mortality occurred during flowering, and clearly if it had been greater a more pronounced parabolic yield curve would have occurred.

Whilst intraspecific competition may act to reduce plant size and reproductive output in relation to the developmental schedule of a plant, it is very commonly observed that the number of seeds produced by a plant bears an exponential relationship to its size whether measured by mass or indirectly in the case of herbs by stem diameter (Fig. 2.11). (This relationship does, however, break down where plants show an age-dependent fecundity schedule as in the case of the trees.)
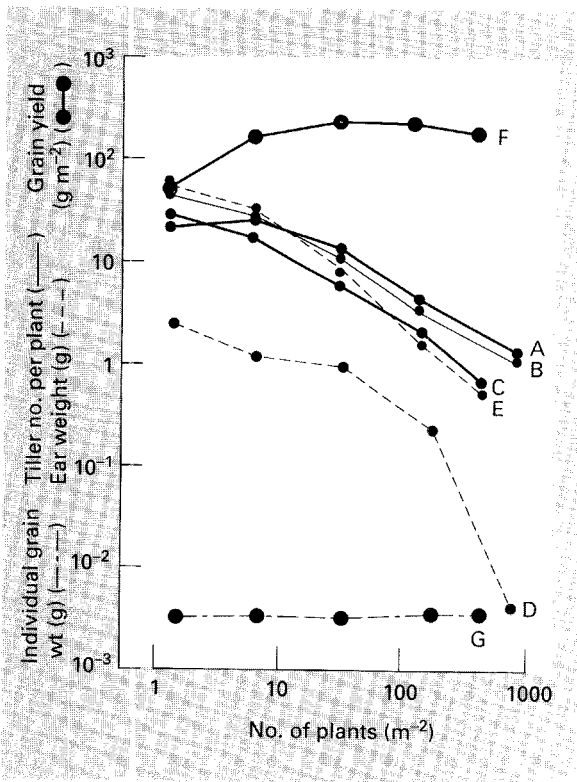
Fig. 2.10 Yield-density relationships in *Triticum aestivum*. (Data from Puckridge & Donald, 1967.) A, tiller number per plant after 14 weeks; B, tiller number per plant after 17 weeks; C, number of fertile tillers per plant after 26 weeks; D, individual ear weight after 17 weeks; E, individual ear weight after 26 weeks; F, total grain yield at 26 weeks; G, individual grain weight after 26 weeks.

2.5.3 Individual variability

Characterizing plant populations by an average response as we have done up to now masks the mechanism by which compensation actually occurs. We must now consider the fates of *individuals* within the population.

Obeid *et al.* (1967) sowed *Linum usitatissimum* (flax) at three densities and harvested at three stages of development, recording the weight of each plant individually. Figure 2.12 makes it quite clear that the frequency distribution of weights is skewed towards the left and that the skewing is increased by the passage of time and by an increase in density. The resulting populations display a few large individuals and a great many small ones. Similar distribution patterns have been observed in the growth of single-species populations of crop plants, mixed tree plantations and in animals (Begon, 1984).

There are two partially interrelated causes of skewness in the size distributions of populations in the absence of the death of plants. Even in plant populations sown at the same time, individuals will germinate at slightly different times, perhaps due to variation in the 'local' environment for germination or because of differences in seed size. These subtle differences in time of birth and size at birth will then become exaggerated as the growth of individuals proceeds. In addition, however, competition may further exaggerate skewness. Larger individuals which will often be those that emerge first will be comparatively unaffected by interference from smaller (and later) neighbours. As a consequence they will grow quickly. Conversely, small plants and late emergers not only have to compete with a number of other, generally larger individuals, but have to do so on unequal terms. Intraspecific competition accentuates initial differences in size: large (early) individuals are least affected by competition and grow larger still; small (late) individuals are most affected, and lag further and further behind. Competition, then, serves to exaggerate size differences that initially may be determined by environmental chance or variation in initial starting capital: seed size.

The inevitable consequence of this process is the development of a population in which size differences will be exaggerated and a left-handed skew will develop. A 'hierarchy of exploitation' will result in a few dominant individuals with high growth rate and disproportionate share of resources whilst 'the most common type of plant in experimental (and natural) plant populations is the suppressed weakling' (Harper, 1977). Experimental support for this view comes from the work of Ford (1975) on sitka spruce (*Picea sitchensis*) (Fig. 2.13). The greatest relative growth rate occurred in trees with the largest girth size, these trees being in the minority.

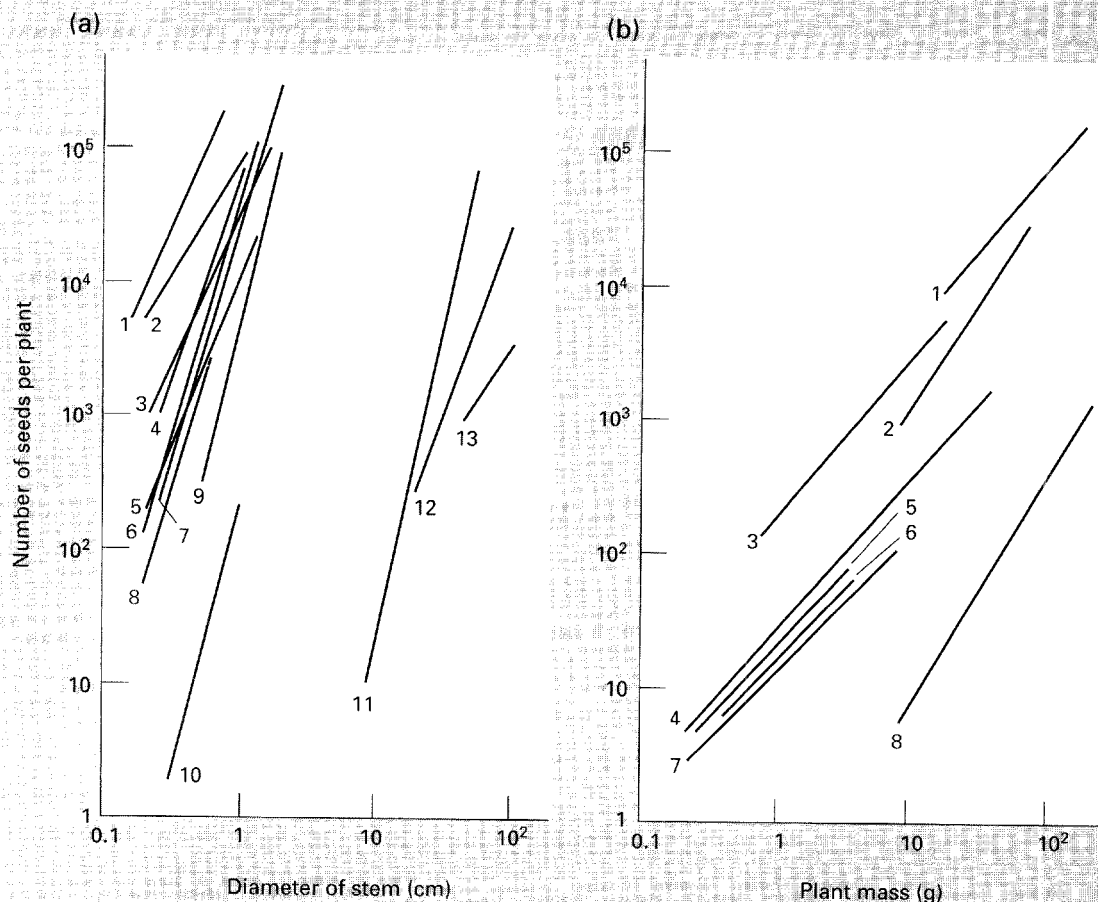Finally we can consider the influence of limiting resources at the level of the modular growth of an

Fig. 2.11 The relationship between fecundity and size in seed plants. Lines show the relationship, on logarithmic scales, between observed sizes of individual plants and seeds produced per plant. In (a) size is expressed as basal stem diameter for herbs (1–9) and a shrub (10) and as diameter at breast height for trees (11–13). In (b) size is measured as above-ground biomass for perennial (1–3) and annual (4–8) species. (After Watkinson & White, 1985.)

organism. Porter (1983b) grew single *Fuchsia* plants in three different soil volumes and examined the accumulation of modules with time. His results (Fig. 2.14) show that whilst growth was initially rapid in all volumes, the onset of a stationary plant size—the plateau phase in the curves—was determined by the amount of soil available. Limiting the resources avail-

able influences the size of the module population and hence individual plant size. If this limitation arises through individuals interfering with resource gathering by one another (intraspecific competition) then differential reductions in relative growth rate amongst plants will occur and be reflected in the absolute size distribution of the population.

2.5.4 Self-thinning in plants

Certain aspects of these results on *Linum* are frequently repeated: the effects of intraspecific competition on a growing plant population often become accentuated with the passage of time. These effects most commonly concern plant density (which de-
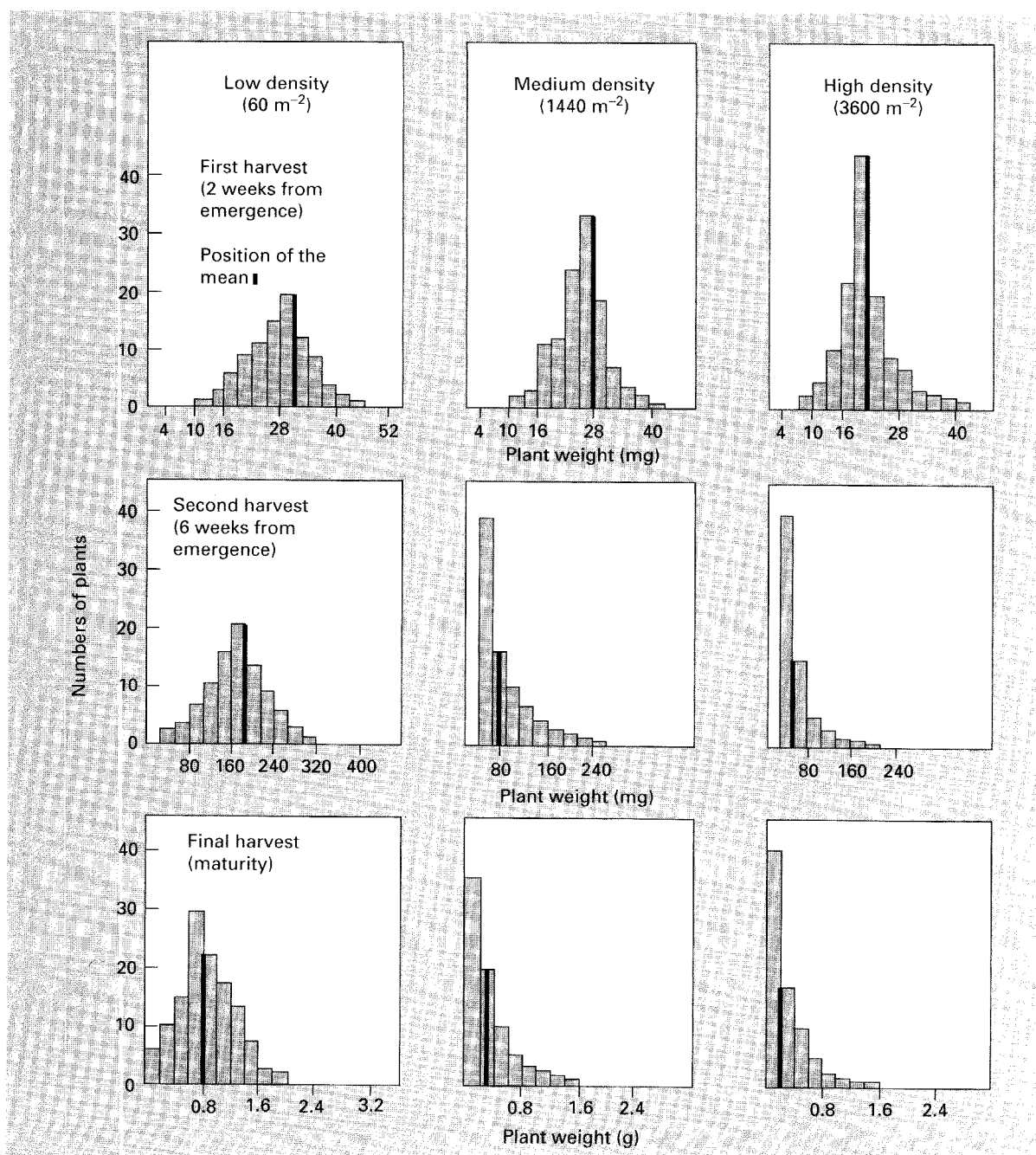
Fig. 2.12 Frequency distributions of plant weights in populations of flax, *Linum usitatissimum*, sown at three densities. (Data from Obeid *et al.*, 1967; after Harper, 1977.)
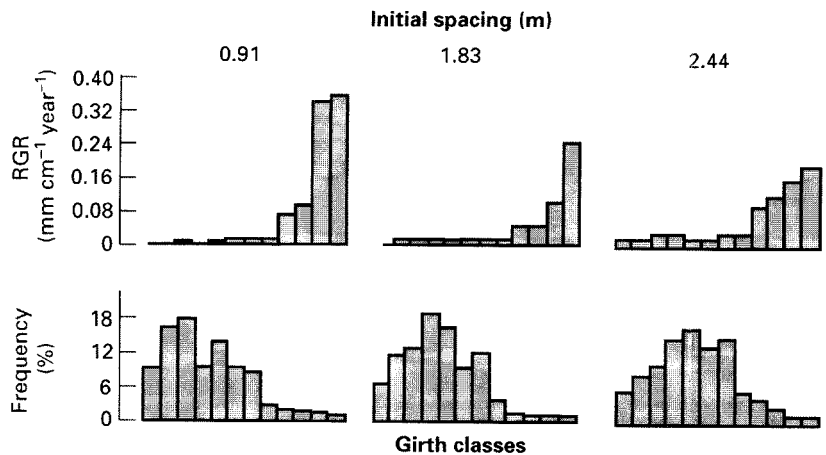
Initial spacing (m)

Fig. 2.13 Relative growth rates (RGR) and frequency distributions of size (12 equal intervals of girth classes) in *Picea sitchensis*, 29 years after planting at three different densities. (From Ford, 1975.)

creases with time), and mean plant weight (which increases with time); these two parameters appear to be closely related. 'Self-thinning' refers to the dynamics of density-dependent mortality that occurs progressively in cohorts as individuals grow in size. It has been studied most often in plant populations in monocultures. The process is well illustrated in an experiment by Kays and Harper (1974) in which they sowed a series of populations of *Lolium perenne*, perennial ryegrass, at densities ranging from 330 to 10 000 seeds m^{-2}, and harvested their populations at subsequent occasions over a period of 180 days. Growth in this species occurs through the accumulation of ramets (shoots or tillers) on the genet (established plant). Throughout the experiment (Fig. 2.15a) there was continual death of genets. Initially, this was most marked at the highest sowing density but latterly it assumed a rate independent of sowing density. During the early part of the experiment the number of ramets per unit area increased but then declined to give a similar number per m^2 after 125 days regardless of initial genet starting density. This constancy was repeated after 180 days but at a lower density. Compensatory processes within the population resulting in this constancy of tiller number derive from differential mortality of genets and differential rates of birth and death of tillers on them (Fig. 2.15a). Plotting the average genet size (mean above-ground plant
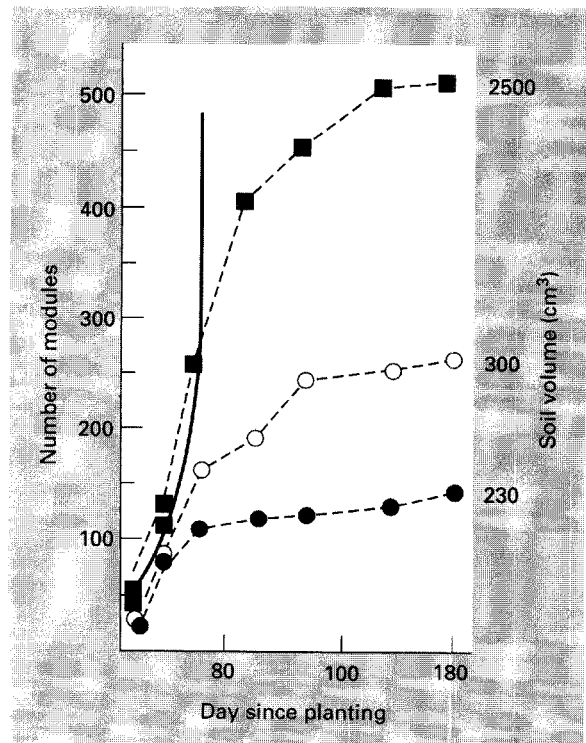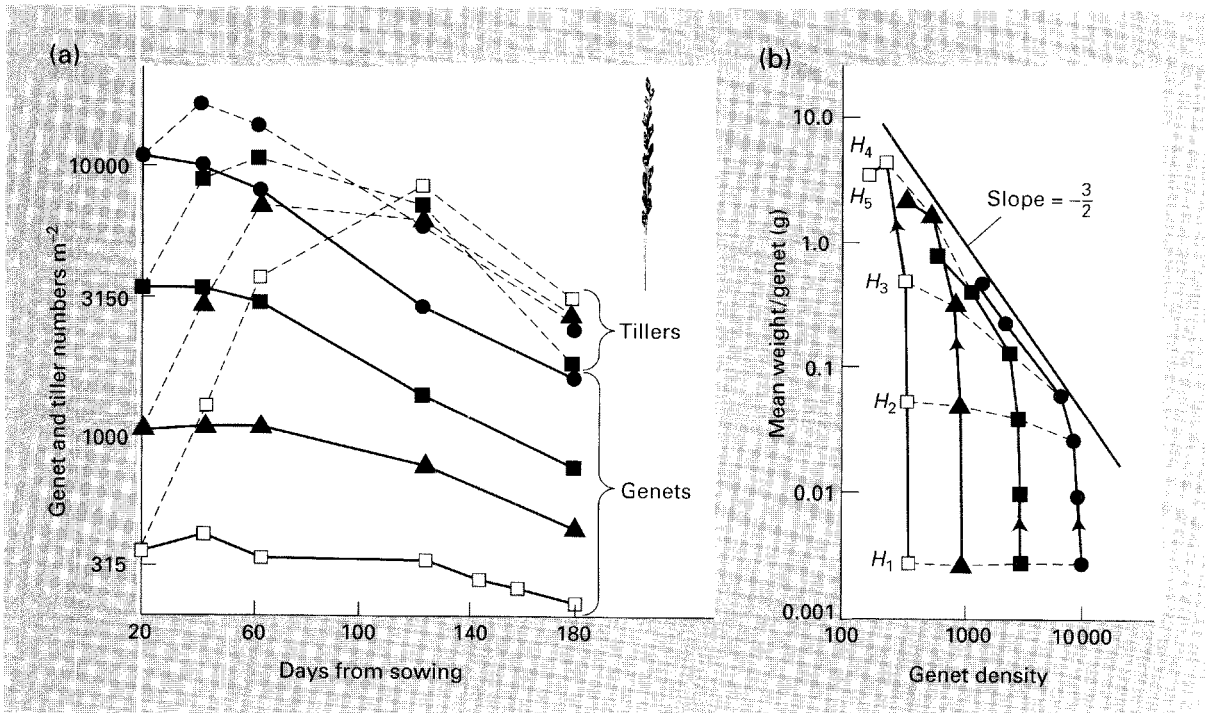

Fig. 2.14 The production of modular units by *Fuchsia* (cultivar Royal Velvet), in different soil volumes. The solid line shows the total number of modules assuming unrestricted exponential growth rate. Plants received abundant water but no additional nutrients. (From Porter, 1983b.)

Fig. 2.15 Intraspecific competition affects tillers more than genets. (a) Changes in tiller and genet density in populations of ryegrass, *Lolium perenne*, sown at a range of densities. (b) The change in genet density and mean genet weight over the course of five harvests (H_1–H_5) for the same ryegrass populations. Arrows indicate progression of time and dashed lines link populations harvested at the same time. (Data from Kays & Harper, 1974; after Harper, 1977.)

biomass) against the density of surviving genets (Fig. 2.15b) we can examine the process of plastic response intertwined with mortality. The essence of studying self-thinning is to examine not a range of initial densities all at one time, but the *time course* of a single initial density as the individuals grow in size. The time courses show that the 'average' genet in a population grows, i.e. increases in biomass (points move upwards in the graph) at a rate diminishing with density (dotted lines curve down), until at a critical size, depending on genet density, further biomass increases can only be achieved with a concomitant loss of genets (points in the diagram shift to the left). Eventually the time courses appear to progress along a line with a gradient of – 1.5.

We have introduced two quite separate descriptions of the manner in which plant populations respond to density: (i) yield-density or competition-density (as they were originally termed by Kira *et al.*, 1953) effects where mortality within the population does not occur; and (ii) the relationship between plant size and population density as self-thinning occurs.

In Fig. 2.7b at each harvest time, the reciprocal relationship between mean plant biomass (w) and the density of plants (N) can be modelled as follows.

$$w = w_m(1 + aN)^b \tag{2.1}$$

where w_m can be interpreted as the yield of a plant isolated from competing neighbours and a and b are parameters that describe the competition effect. b has been variously interpreted as the rate at which the effects of competition change with density (Vandermeer, 1989), or the efficiency of resource utilization (Watkinson, 1984). These interpretations are, at best, attempts to associate biological meaning to the parameter b in an empirical model and we will return to their return to their functional interpretation in Chapter 3. When $b = 1$, there is exact weight-density

compensation and a plot of log mean weight against log density has a slope of -1. Values of all three parameters (W_m, a and b) will increase during the course of plant growth and the change in a and b will be more rapid when the total availability of resources is least. Figure 2.16 shows competition-density effects in *Vulpia fasiculata* populations grown at three fertilizer levels; note that values of b change more quickly when plants are grown at low fertilizer levels.

The relationship between average plant size and the number of survivors in a self-thinning population can be described by

$$w = cN^{-k} \tag{2.2}$$
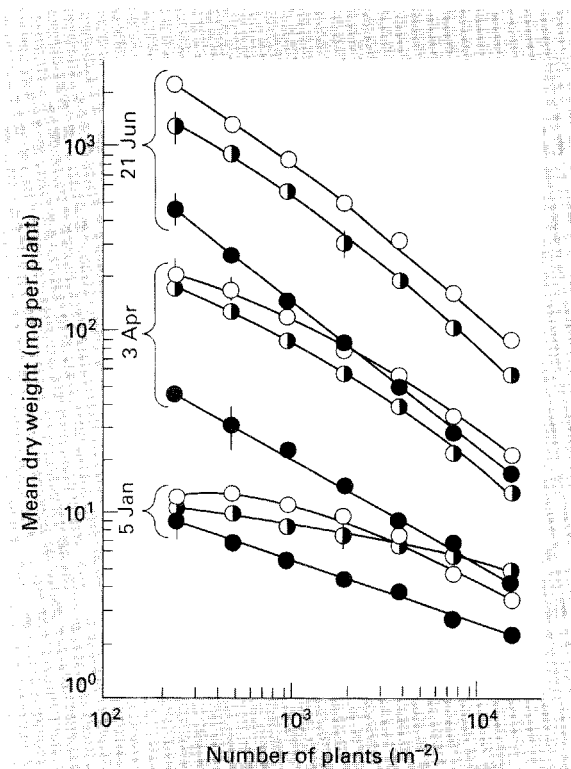
or

$$\log(w) = \log c - k \log N \tag{2.3}$$

Fig. 2.16 The influence of density and low (●), medium (◑) or high (○) nutrient regime on the shoot dry weight per plant of *Vulpia fasiculata* at three successive harvests. Note how the lines become steeper as mean plant size increases. (From Watkinson, 1984.)

where w and N are as defined above. However, it is crucial to emphasize that this description is only appropriate when the population is *undergoing density-dependent mortality*. Originally, Yoda *et al.* (1963) proposed that the exponent k had a fixed value of -1.5 and the relationship was described as the self-thinning rule or the '$-3/2$ power law'. The implication of this rule is that the self-thinning line represents a boundary condition that is common to all plant species. This implication and the interpretation and biological significance of k and c has been a matter of strong debate (see Westoby, 1984; Lonsdale, 1990). There are two major strands of evidence that support the view that there is an inverse relationship between mean plant weight and density with a slope of approximately $-3/2$. The first is that the relationship exists for a great many species widely differing in overall size and form (Fig. 2.17).

The second is based around the explanation of the value of $3/2$ on physical grounds. The biomass of a plant will be proportional to its volume and in turn the volume occupied will be proportional to the spatial area in which the plant is growing. This area is inversely related to density. Biomass will therefore be inversely related to density according to a function determined by the volume to area ratio. As volume is a cubic and area is a squared dimension the power will be $3/2$. Thus as individuals grow in a self-thinning population their 'areas' increase by a power of 2, their densities decrease by a power of $1/2$ but their mean biomass increases by a power of 3. Burrows (1991) provides a detailed geometric explanation of the $-3/2$ thinning rule based on considerations of canopy volume.

From a number of studies it has been found that the values of k fall in the range between 1.3 and 1.8 on log–log plots of mean plant biomass against density of survivors (White, 1980). The universality of the $-3/2$ thinning rule, therefore, has been questioned by a number of workers on the grounds that some species significantly deviate from the $3/2$ relationship (Zeide, 1987; Weller, 1990) and that the line represents a boundary rather than a course along which self-thinning populations will progress (White, 1985). In a careful review, Lonsdale (1990) concluded that there were too many examples in which a slope of $3/2$ was
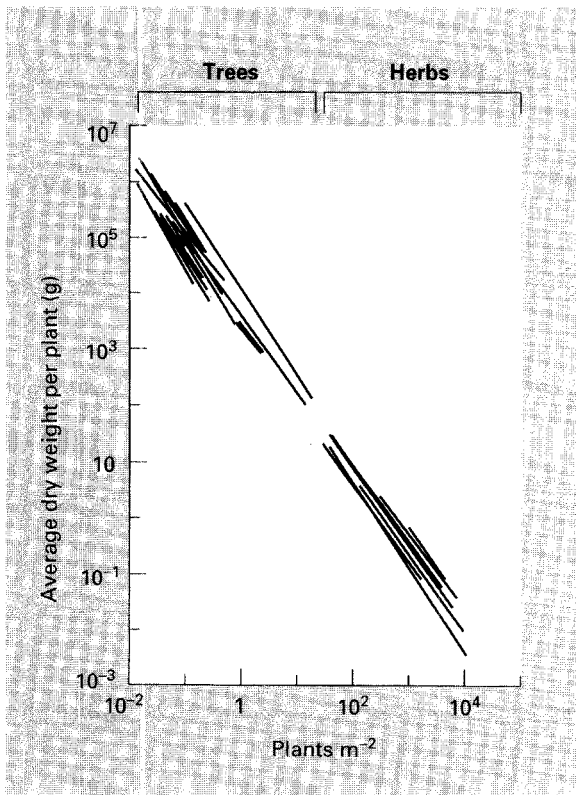
Fig. 2.17 The relationship between average plant weight and surviving plant density in self-thinning populations of trees and herbs. Each line represents a different species in a total of 30. (After White, 1980.)

not found to justify the claims of universality for the rule. It has been shown (Osawa & Sugita, 1989) that plant mortality often occurs in the approach to the self-thinning line (see data points H_3 and H_4 in Fig. 2.15b) and it may well be that this phenomenon can explain measurement of slopes of steeper than $-3/2$. Finally, we must note that a slope of $-3/2$ indicates that the increase in mean biomass of a plant in a self-thinning population is faster than the reduction in density due to mortality. However, yield cannot indefinitely increase, since in every environment there will be a maximum total yield that a species may achieve. In this situation we might expect the thinning line to have a slope of -1 indicating that the total yield per unit area remains constant. Lonsdale and

Watkinson (1982) grew *Lolium perenne* at densities at which self-thinning occurred and observed the trajectories of populations at both full and low (17%) light. At low light, the maximum yield attainable was reduced and interestingly populations self-thinned with a trajectory of -1. In contrast, under high light a slope of $-3/2$ was observed. It thus seems possible that self-thinning may occur at two different rates but no plant population yet has been observed to make the switch.

The ' $-3/2$ law' remains a matter of debate amongst plant ecologists and development of our understanding will probably only come with a deeper knowledge of the mechanisms of competition and greater attention to variation in the performance of individuals. (Charles-Edwards, 1984; Firbank & Watkinson, 1985; and Hara, 1988 provide launch points for the interested reader.)

In summary, we have seen how work on intraspecific competition in plants has established that the responses of actual populations are far more complex than was envisaged for 'scramble' and 'contest'. There is little uniformity of response from plant to plant, and the quality, as well as the quantity, of surviving individuals is affected. As a consequence, there is no sudden threshold of response. Plants show these features particularly clearly; it is appropriate, now, to examine some zoological examples.

2.5.5 Competition in *Patella cochlear*

Branch (1975) studied the effects of intraspecific competition on the limpet *Patella cochlear*, making observations on natural populations in South Africa varying in density from 125 to 1225 m^{-2}. This species feeds mainly on the alga, *Lithothamnion*, which grows not only on the limpets' rocky substrate, but also on the limpet shells themselves. Thus, the total amount of food (based on the total surface area) remains approximately constant. As density rises, however, the juvenile limpets increasingly live and feed on the shells of adults, so that competition for space is largely eliminated. But there is ever more intense competition for food. Some of Branch's results are illustrated in Fig. 2.18.
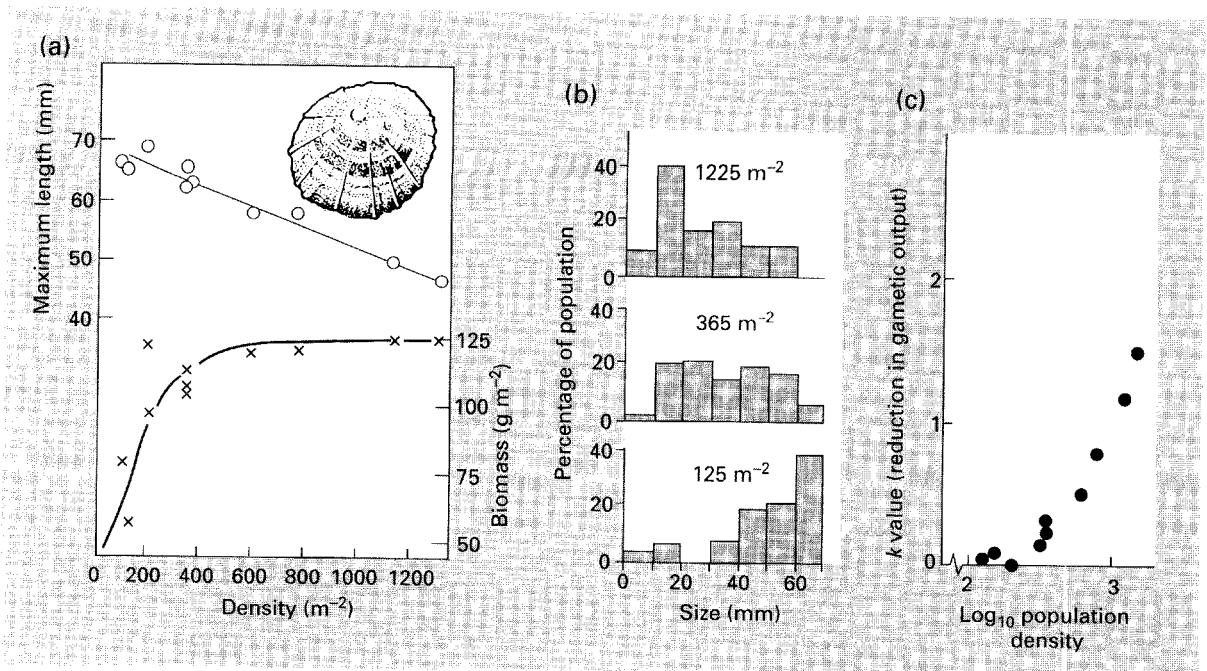
Fig. 2.18 Intraspecific competition in a limpet. (a) Maximum length (○) and biomass (×) of the limpet, *Patella cochlear*, in relation to density. (b) Size distributions of the limpets at three densities. (c) The effect of intraspecific competition on the limpets' gametic output. (Data from Branch, 1975.)

Figure 2.18a shows that as density increases, there is a compensatory reduction in limpet size, leading to a stabilization of the total biomass at around 125 g m^{-2} for all densities in excess of around 450 m^{-2}. The regulatory properties of intraspecific competition and the plasticity of individual response are both readily apparent. It is clear from Fig. 2.18b, however, that consideration of only the mean or the maximum size of limpets would be very misleading; the size distribution undoubtedly alters as density increases. The reason appears to be that at low densities there is little juvenile mortality, most individuals reach the adult stage, and (large) adults come to dominate the population. As density and intraspecific competition increase, however, there is increased juvenile mortality and decreased rates of growth, so that at high densi-

ties there are comparatively few (large) adults. Once again, the effect of intense intraspecific competition is a population dominated (numerically) by suppressed weaklings.

Branch had previously established that larger animals produce proprtionally more gametes. Thus, the changing size distribution of the population, despite the stabilization of biomass, would be expected to lead to a reduced gametic output as density increased. This is confirmed in Fig. 2.18c, where once again the use of k-values has proved instructive. At low densities (where there is little evidence of a sudden threshold) the reduction in size does not compensate for the increase in density ($b < 1$), and the total gametic output increases. However, at high densities there is increasing *over*compensation ($b > 1$), and the total gametic output decreases at an accelerating rate. Once again, there is a moderate density (around 430 m^{-2}), at which $b = 1$ and the gametic output is at its maximum. The ultimate, regulatory effects of intraspecific competition are acting on the contributions of limpets to future generations.

2.5.6 Competition in the fruit fly

As a second zoological example, we will consider the experimental work of Bakker (1961) on competition between larvae of the fruit fly, *Drosophila melanogaster*. Bakker reared newly hatched larvae at a range of densities. Some of his results are illustrated in Fig. 2.19. As far as larval mortality is concerned, intraspecific competition appears to approach pure scramble. There is a sudden threshold at a density of around 2 larvae mg^{-1} yeast, and mortality thereafter very quickly reaches 100%. But the simplicity of this situation—and its similarity to pure scramble—is very largely an illusion. Up to the threshold density, competition has little or no effect on larval mortality; but the growth-rate of the larvae is very much affected, as is their final weight at pupation. Moreover, it is well known that in *D. melanogaster* small larvae lead to small pupae, which lead to small adults; and that these small adults, if female, produce comparatively

few eggs. As Fig. 2.19 shows, with increasing larval density there is a decrease in the size of adults produced; this will lead to a decrease in the number of eggs contributed to the next generation. Hence, even below the threshold for the larval mortality, intraspecific competition is exerting a density-dependent regulatory effect on the *D. melanogaster* larvae. But it is the quality, not the quantity, of larvae which is affected, and, ultimately, their contribution to the next generation which is reduced. Above the mortality threshold, the larvae are so reduced in size that they are not even large enough to pupate; when this happens they eventually die.

Clearly, in animals as in plants, intraspecific competition is very much more complicated than scramble or contest. Moreover, the complications—lack of a sudden threshold, individual variability and so on— are very largely the same in both major kingdoms.

2.6 Negative competition

Finally, we need to consider an interaction which is beyond the spectrum of intraspecific competition dealt with so far. It is an example of a situation in which fecundity *increases* (or mortality decreases) with rising density. Birkhead (1977) studied breeding success in the common guillemot (*Uria aalge*) on Skomer Island, South Wales. The birds breed there in several sub-colonies of differing density. Female guillemots lay just one egg, and a pair of birds can be considered successful if they rear their chick until fledging. By visiting the various sub-colonies at least once a day throughout the breeding season, Birkhead was able to make careful observations on the losses of eggs and chicks, and could compute the percentage of pairs breeding successfully. His results are shown in Fig. 2.20. It is quite clear that as density increases, breeding success, and thus fecundity, also increases. This is a case of inverse density-dependence. Competition is actually negative, and might more properly be called cooperation. Indeed, cooperation does appear to be the explanation for these results. Great black-backed and herring gulls are both important predators of the eggs and chicks of guillemots on Skomer, and denser groups are less susceptible to predation.
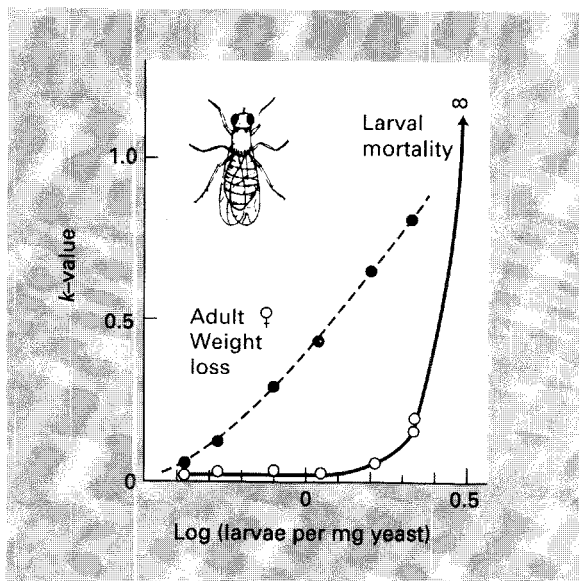

Fig. 2.19 The effects of intraspecific competition for food in the fruitfly *Drosophila melanogaster*. For adult weight loss, a variable number of larvae competed for a constant amount of food. For larval mortality, a constant number of larvae were given a variable amount of food. (Data from Bakker, 1961; after Varley *et al.*, 1975.)
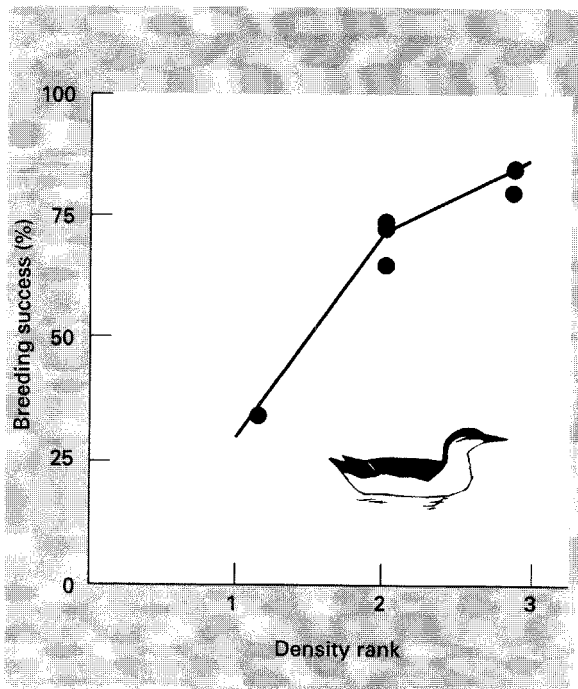
CHAPTER 2: INTRASPECIFIC COMPETITION 51

Fig. 2.20 Cooperation: the effect of density on breeding success in subpopulations of the common guillemot *Uria aalge* on Skomer. (Data from Birkhead, 1977.)

Fig. 2.21 The 'Allee effect' (Allee, 1931). Density-dependent birth at moderate and high densities leads to a stable carrying-capacity, *K*, but the change to inversely density-dependent birth at low densities leads to an unstable equilibrium, *U*, below which the population will decline to extinction (see also Fig. 2.2).

because a number of guillemots are able (together) to deter gulls by lunging at them. Thus, our spectrum of competition (and density-dependence) must for completeness, be extended to 'cooperation' and inverse density-dependence. Not surprisingly, just as there is a regulatory tendency associated with density-dependence, there is a destabilizing tendency associated with inverse density-dependence. This is illustrated diagrammatically for the guillemots on the left-hand side of Fig. 2.21, in which birth-rate rises
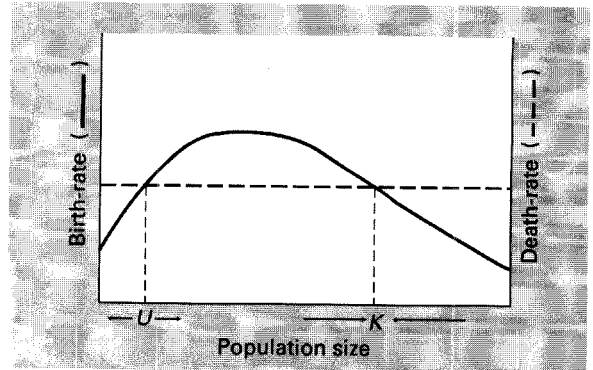
with density while death-rate remains constant. Small populations get smaller still (because death-rate exceeds birth-rate), while larger populations increase in size (because birth-rate exceeds death-rate). However, it is likely that these destabilizing tendencies will disappear and then be reversed as population size increases and the carrying-capacity is approached. The situation over all densities, therefore, is likely to be as illustrated in the whole of Fig. 2.21, and is known as the 'Allee effect' (Allee, 1931). The regulatory density-dependent effects to the right of the figure are easy to image. The destabilizing inversely density-dependent effects to the left of the figure could result from cooperation (as with the guillemots), or from certain other problems associated with low density (mate-finding, for instance). We shall consider the Allee effect again in section 5.13.3.